Ann. Natal Mus. Vol. 36 Pages 147–159 Pietermaritzburg October, 1995

The internal female genital organs of *Chaetodiopsis* and *Diasemopsis* (Diptera: Diopsidae) and their systematic relevance

by

Marion Kotrba
(National Museum of Natural History, NHB 169, Washington, D. C., 20560 USA)

ABSTRACT

The morphology of the internal female reproductive organs of *Chaetodiopsis meigenii* and four *Diasemopsis* species, all based on material from Natal (South Africa), is described. Variation is evident, especially in the form and size of the ventral receptacle, the ventral sclerite, and the spermathecae. Phylogenetic analysis of these characters, in combination with results available from other diopsids, resolves generic but not species relationships. It confirms that this character system can be valuable for phylogenetic analysis, as suggested by previous authors.

The vast enlargement of the multi-chambered ventral receptacle in *Chaetodiopsis* and *Diasemopsis* has various implications on the possibilities of sperm competition and spermatozoa selection, that deserve further investigation. The ventral receptacle possibly acquires part of the sperm storage function from the spermathecae, that are concurrently reduced in number and size. Furthermore, the parallel arrangement of several hundred chambers, housing individual spermatozoa, provides an arena for spermatozoa competition. The elongation of the chambers, coinciding with the elongation of the spermatozoa, constitutes a new example for the coevolution of spermatozoa and female sperm receptacles.

INTRODUCTION

The female reproductive system of Diptera has received little study, although preliminary studies indicate that it is the source of valuable new characters for resolving phylogenetic relationships within the order (Sturtevant 1925 1926, Hennig 1973, McAlpine 1989, Griffiths 1990, Kotrba 1993). Moreover, detailed knowledge of the functional morphology of these organs is the key to understanding possibilities of postcopulatory sexual selection, such as sperm competition and female sperm selection – currently active topics in evolutionary biology (Smith 1984, Eberhard 1985, Simmons & Parker 1992, La Munyon & Eisner 1993, Ward 1993). This paper contributes to our knowledge of these topics, with a specific focus on the family Diopsidae (Schizophora).

Diopsidae, or stalk-eyed flies, are characterised by lateral head protrusions bearing the compound eyes and antennae. The family includes 12 recent genera with approximately 170 described species, the majority of which occur in subsaharan Africa (Feijen 1989). A few species are considered pests of rice and other gramineous crops. The mating system of Diopsidae has received considerable attention. It involves male competition and female choice at nocturnal aggregation sites (Burkhardt *et al.* 1994, Wilkinson & Reillo 1994).

Very little, however, is known about the internal female reproductive system of Diopsidae. Reports are mostly confined to the sclerotised spermathecae (Tenorio 1969, Feijen 1981 1984 1986). Figures of *Diasemopsis meigenii* (placed in the monotypic genus *Chaetodiopsis* by Feijen (1989)), *Diopsis thoracica* and *Diopsis cf.*

circularis show the spermathecae and a more or less ring-shaped structure, whose alignment with the rest of the vagina remains unclear (van Bruggen 1961). In Tan's (1965) illustration of *Diopsis subnotata*, a sclerotised ring is located in the ventral wall of the vagina and three spermathecae are connected to its dorsal wall. Publications on *Diopsis thoracica* (see Kumar & Nutsugah 1976) and *Sphyracephala hearseyana* (see Kumar 1978) show schematic views of the vagina, spermathecae and accessory glands. However, none of these authors mentions a ventral receptacle.

A detailed investigation of the reproductive system of *Cyrtodiopsis whitei* from Malaysia, recently revealed the presence of a multi-chambered ventral receptacle in the anterior portion of the vagina that functions as the fertilization site (Kotrba 1993). Other remarkable findings were that *C. whitei* also possesses a ring-shaped sclerite in the ventral wall of the vagina, encircling a cushion of specialized epithelium, and that sperm is transferred by spermatophores in this species (Kotrba 1990 1993). Since then other diopsids have been investigated comparatively to resolve the distribution of these features within the family. A publication reporting the occurrence of spermatophores in *Diasemopsis* and other genera of Diopsidae is in preparation. In this paper I describe the female reproductive organs of *Chaetodiopsis meigenii* (Westwood, 1837), *Diasemopsis dubia* (Bigot, 1874), *D. munroi* Curran, 1931, *D. obstans* (Walker, 1861), and *D. silvatica* Eggers, 1916, which were collected and investigated whilst at the Natal Museum in Pietermaritzburg.

Both of the last-mentioned genera belong to the *Diasemopsis* genus group (Feijen 1989). Although they share many characters with *Cyrtodiopsis whitei*, those that distinguish them are informative in terms of phylogeny as well as functional morphology. Fewer spermathecae, from three to two, is already known to constitute an important synapomorphy of the *Diasemopsis* genus group (Feijen 1989). Yet most remarkable is the vast enlargement of the multi-chambered ventral receptacle through multiplication and elongation of its chambers. The latter seems to have coevolved with spermatozoa elongation.

MATERIALS AND METHODS

The specimens used in this study were collected in the vicinity of Pietermaritzburg (South Africa) during April and May 1992. They were determined by the author through comparison with the original species descriptions. *Diasemopsis dubia* and *D. silvatica* were reared in culture as part of the investigation on the occurrence of spermatophores and spermatozoa morphology.

For the morphological description three to four specimens per species were killed in 70 % ethanol and dissected either immediately or after being fixed for a few hours. The internal reproductive tract was removed and embedded in Polyvinyllactophenol with an admixture of Chlorazol Black E. This medium slowly macerates soft tissue while staining unsclerotised cuticular parts blue. Living spermatozoa were retrieved from the ventral receptacle of mated females. Their length was measured in smears, that had been dried, heat fixed and stained in Toluidine Blue. A Zeiss Axioskop equipped with a M 35 W camera was used to take photographs on Agfa Diadirekt black and white film. Drawings were made using a Wild Heerbrugg M 20 EB compound scope with drawing tube.

The characters of the internal female reproductive tract were evaluated using Hennig86 (Farris 1988). *Cyrtodiopsis whitei* (see Kotrba 1993) and *Teleopsis quadriguttata* (see Tan 1965, Kotrba unpublished data) were used as outgroups. They are considered to be relatively closely related to the *Diasemopsis* genus group (Steyskal 1972, Feijen 1989).

RESULTS

The description comprises those parts of the internal female reproductive tract that are of ectodermal origin and therefore internally lined with cuticle: namely the common oviduct, the vagina, the spermathecae, the accessory glands and the ventral receptacle. The coding of these characters for phylogenetic analysis is presented in table 1. Reference should be made to Figures 1–22 when reading and evaluating the descriptive text.

The **vagina** is an elongate tube, wider and very muscular in its anterior region, but tapered towards the vulva. When empty, its dorsal wall is concave, so that it lies close to the ventral wall. The lumen is confined to a narrow cleft. The anterior end of the vagina is connected to the **common oviduct**, which descends from the paired ovaries and lateral oviducts. The posterior end is attached to the vulva behind sternum eight. A pouch-like evagination of the dorsal anterior portion of the vagina receives the spermathecal ducts and, posterior to them, the ducts of the accessory glands. Directly opposite the entrance of the spermathecal ducts, the ventral receptacle emanates from the ventral anterior portion of the vagina.

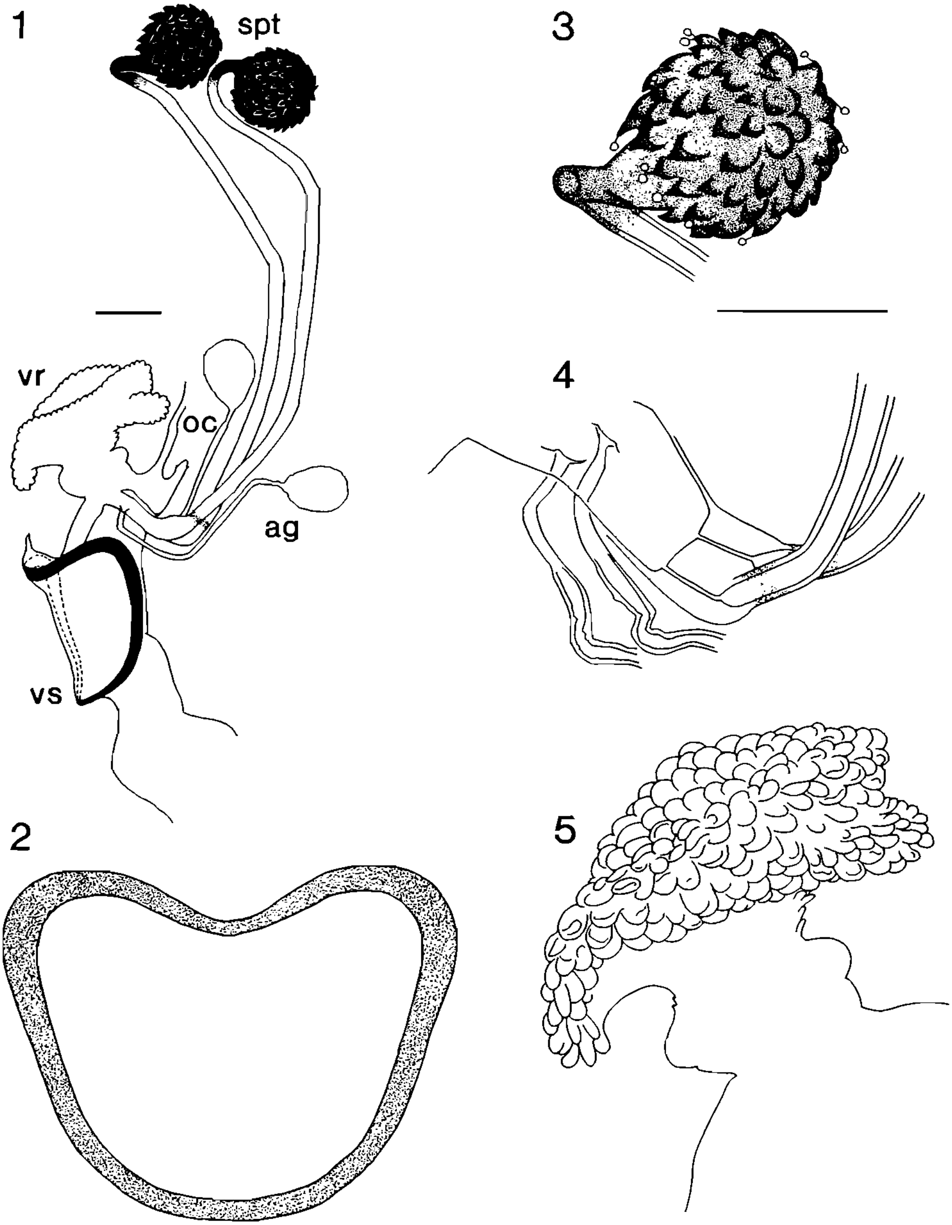
A ring-shaped **ventral sclerite** is embedded in the ventral wall of the posterior portion of the vagina. Considerable parts of vaginal musculature insert on this sclerite, thus sparing a cushion of specialised epithelium within its centre (Kotrba 1993). The ventral sclerite shows considerable variation in size and shape, forming a narrow longitudinal triangle in *Diasemopsis munroi*, while it is much wider, trapezoidal to almost rectangular in the other four species.

Two **spermathecae** of varying size and shape are present. While they are primarily a slightly enlarged and sclerotised apical portion of the spermathecal ducts in *Diasemopsis dubia*, *D. obstans* and *D. silvatica* (diameter *ca* 40–60 μm), they are spherical with a smaller diameter (30 μm) in *D. munroi* or a much larger diameter (120 μm) in *Chaetodiopsis meigenii*. The spermathecae bear several pointed hollow processes, each connected with up to six cuticular end apparatuses of gland cells (Noirot & Quennedy 1974, Kotrba 1993). The bases of the spermathecae are not telescoped.

The **spermathecal ducts** are comparatively wide in *Diasemopsis*. In *Chaetodiopsis meigenii* they are narrower and longer, and their apical portions are bent proximally. The bases of the spermathecal ducts are weakly sclerotised. In all five species the spermathecal ducts open close to each other, but separately, into a pouch formed by the dorsal wall of the vagina (Figs 1 & 4).

The lumen of the two **accessory glands** is lined by very delicate cuticle and surrounded by glandular epithelium. The conspicuous cuticular end apparatuses of the gland cells are very similar to those associated with the spermathecae.

The **ventral receptacle** is composed of several hundred thin-walled, tubular chambers in all five species. Emanating from a region near the base of the receptacle, these tubules are twisted into a wide spiral, forming a large bulb. The shape of the



Figs 1–5. Internal female reproductive organs of *Chaetodiopsis meigenii* (Westwood, 1837). 1. Lateral view. 2. Ventral sclerite. 3. One of the two spermathecae. 4. Dorsal evagination with openings of spermathecal and accessory gland ducts. 5. Ventral receptacle. [Abbrevations: ag = accessory glands; oc = oviductus communis; spt = spermathecae; vr = ventral receptacle; vs = ventral sclerite. Scale bar = 100 μm, Figs 2–5 at same scale.]

bulb varies from hemispherical in *Diasemopsis dubia*, *D. obstans* and *D. silvatica* to oval in *D. munroi*, and flattened in *Chaetodiopsis meigenii*. The individual tubules measure about 10 μm in diameter and 300–400 μm in length.

In mated females of *Diasemopsis dubia* and *D. silvatica*, individual coiled **spermatozoa** could be detected within the chambers of the ventral receptacle. When freed from the ventral receptacle, the filamentous spermatozoa were extremely long (Fig 18). Their overall length could not be measured, as it was impossible to separate individual spermatozoa from the entangled mass. The longest part of a spermatozoon that could be measured in *Diasemopsis dubia*, was 1150 μm.

TABLE 1

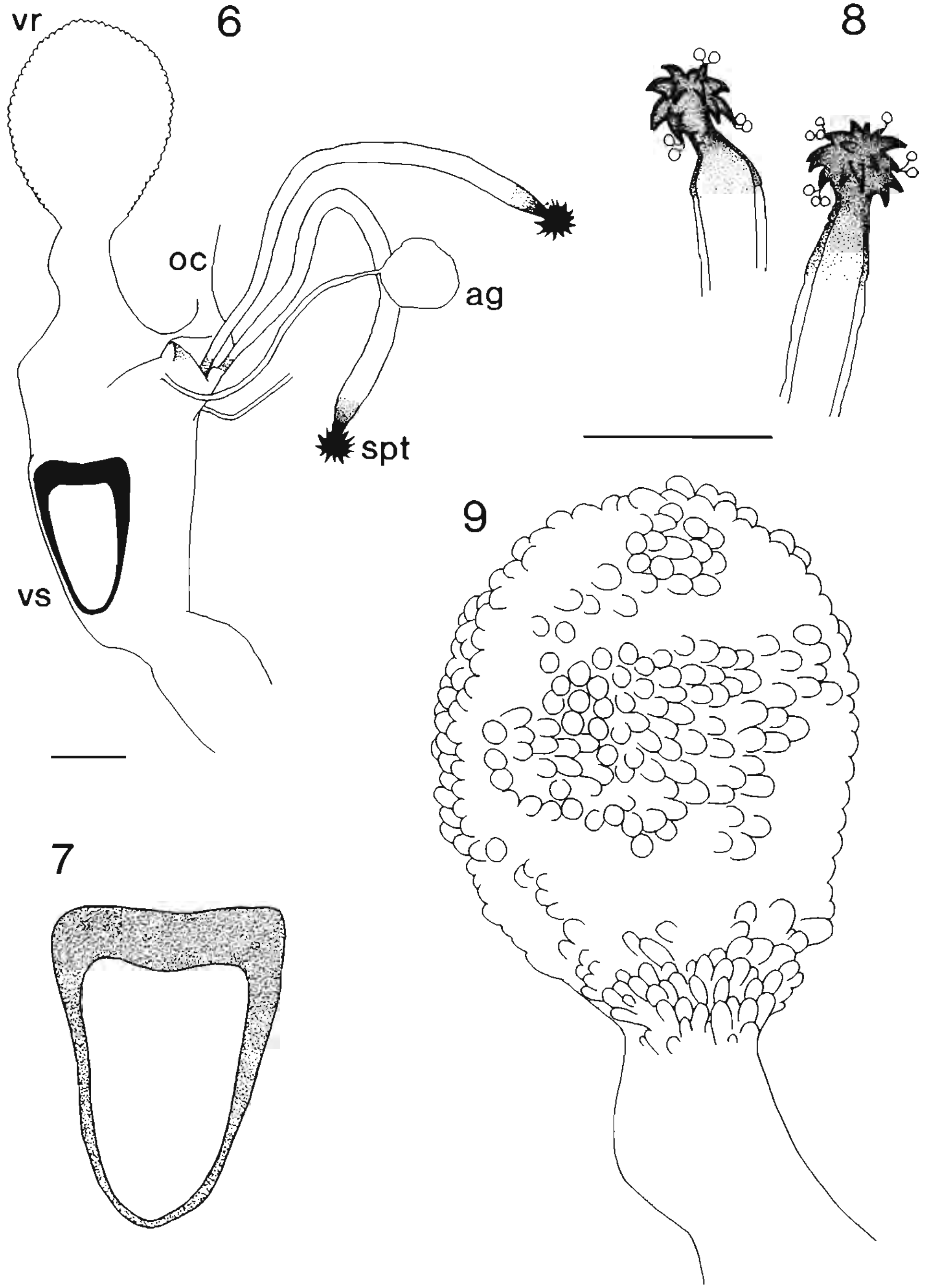
Morphological characters of the internal female reproductive organs of selected diopsid species
0 = plesiomorphic condition; 1, 2 = apomorphic conditions. Characters 3 and 8 are unordered, all others are ordered.

1 Apical end of spermathecal ducts bent (0); apical end of spermathecal ducts straight and relatively wide (1).
2 Hollow processes of spermathecae connected with one gland cell each (0); hollow processes of spermathecae connected with up to 3 gland cells each (1); hollow processes of spermathecae connected with up to 6 gland cells each (2).
3 Bulb of ventral receptacle flattened (0); bulb of ventral receptacle hemispheroid (1); bulb of ventral receptacle ovoid (2).
4 Ventral sclerite narrow (0); ventral sclerite broad (1).
5 Roundish spermathecae much wider than end of spermathecal ducts (0); base of spermathecae merge smoothly with wide ends of spermathecal ducts (1); small spermathecae separated from ducts by constriction (2).
6 Ventral receptacle with about 60 roundish chambers (0); ventral receptacle with several hundred tubular chambers (1).
7 Three spermathecae present (0); two spermathecae present (1).
8 Spermathecal ducts open into base of a protruding genital papilla (0); spermathecal ducts open into base of a vaginal evagination (1).
9 Spermathecal surface smooth (0); spermathecal surface ornamented with hollow processes (1).
10 Ventral receptacle one-chambered (0); ventral receptacle multi-chambered (1).
11 No sclerite embedded in ventral wall of vagina (0); ring-shaped sclerite embedded in ventral wall of vagina (1).
12 Apical pole of spermathecae rounded (0); apical pole of spermathecae pointed (1).

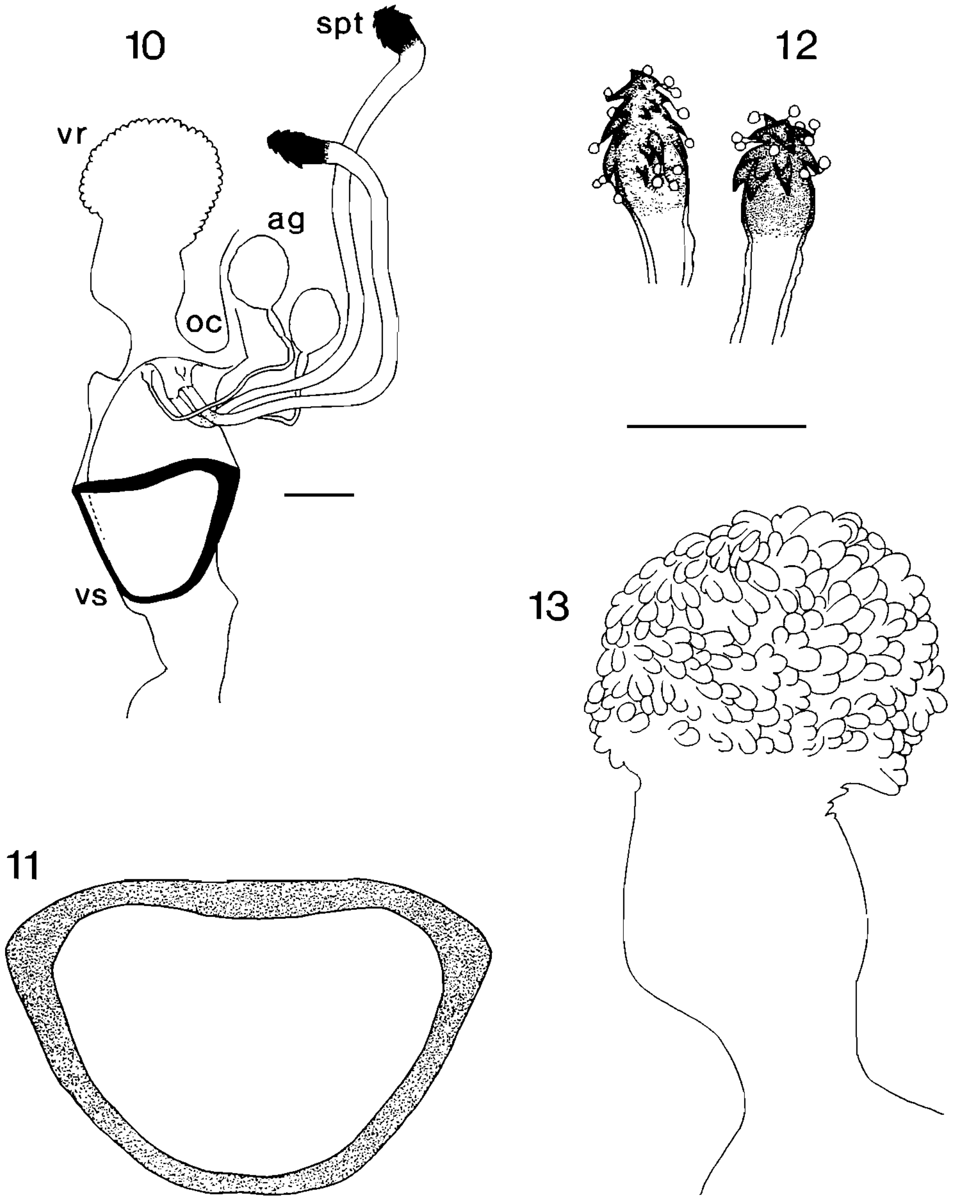
DISCUSSION

Aspects of phylogeny

The reported characters of the internal female reproductive tract of *Diasemopsis* and *Chaetodiopsis* were combined with information available from *Cyrtodiopsis whitei* (see Kotrba 1993) and *Teleopsis quadriguttata* (see Tan 1965, Kotrba unpublished data) in a phylogenetic analysis by Hennig 86. One of the resulting two trees, congruent with the strict consensus tree, is presented in Figure 23. It supports *Chaetodiopsis* as distinct from but closely related to *Diasemopsis*, as suggested by Feijen (1989). The relationships within *Diasemopsis* are not resolved. The results indicate that variation of characters of the female reproductive tract reflect phylogenetic relationships at generic rather than species level. However, the analysis remains preliminary until more species of *Diasemopsis* as well as members of the other genera of the *Diasemopsis* genus group, *Trichodiopsis* and *Cobiopsis*, can be included. Also, to attain a better resolved and more reliable phylogeny, the data should be interpreted in conjuction with other data sets, e.g. from external morphological characters.



Figs 6–9. Internal female reproductive organs of *Diasemopsis munroi* Curran, 1931. 6. Lateral view. 7. Ventral sclerite. 8. Spermathecae. 9. Ventral receptacle. [Abbrevations: ag = accessory glands; oc = oviductus communis; spt = spermathecae; vr = ventral receptacle; vs = ventral sclerite. Scale bar = 100 μm, Figs 7–9 at same scale.]



Figs 10–13. Internal female reproductive organs of *Diasemopsis obstans* (Walker, 1861). 10. Lateral view. 11. Ventral sclerite. 12. Spermathecae. 13. Ventral receptacle. [Abbrevations: ag = accessory glands; oc = oviductus communis; spt = spermathecae; vr = ventral receptacle; vs = ventral sclerite. Scale bar = 100 μm, Figs 11–13 at same scale.]

The *Diasemopsis* species are characterised by the wide, straight apical portion of the spermathecal ducts (character 1-1) and the spermathecal processes being connected with up to six gland cells each (2-2). These features are present in all four *Diasemopsis* species investigated and also in *D. fasciata* and *D. macrophthalma*

(Feijen 1986). Within *Diasemopsis*, the species *silvatica*, *dubia* and *obstans* are most similar, due to the hemispheroid ventral receptacle (3-1), the broad ventral sclerite (4-1), and the bases of the spermathecae merging evenly with the wide apices of the spermathecal ducts (5-1, similar to the spermathecae of *Diasemopsis fasciata* and *D. macrophthalma* (Feijen 1986)). However, these characters are probably symplesiomorphic with respect to *D. munroi*. *D. munroi* is distinguished by derived character states, such as the ovoid vental receptacle (3-2) and the very small spermathecae (5-2), and by the possibly plesiomorphic narrow ventral sclerite (4-0). The shape of the enlarged ventral receptacle (3-0,1,2) is not informative in this respect, as it is not comparable with the small ventral receptacle present in the outgroups. Thus it cannot be decided whether *D. munroi* is positioned at the base of the genus or nested somewhere within it.

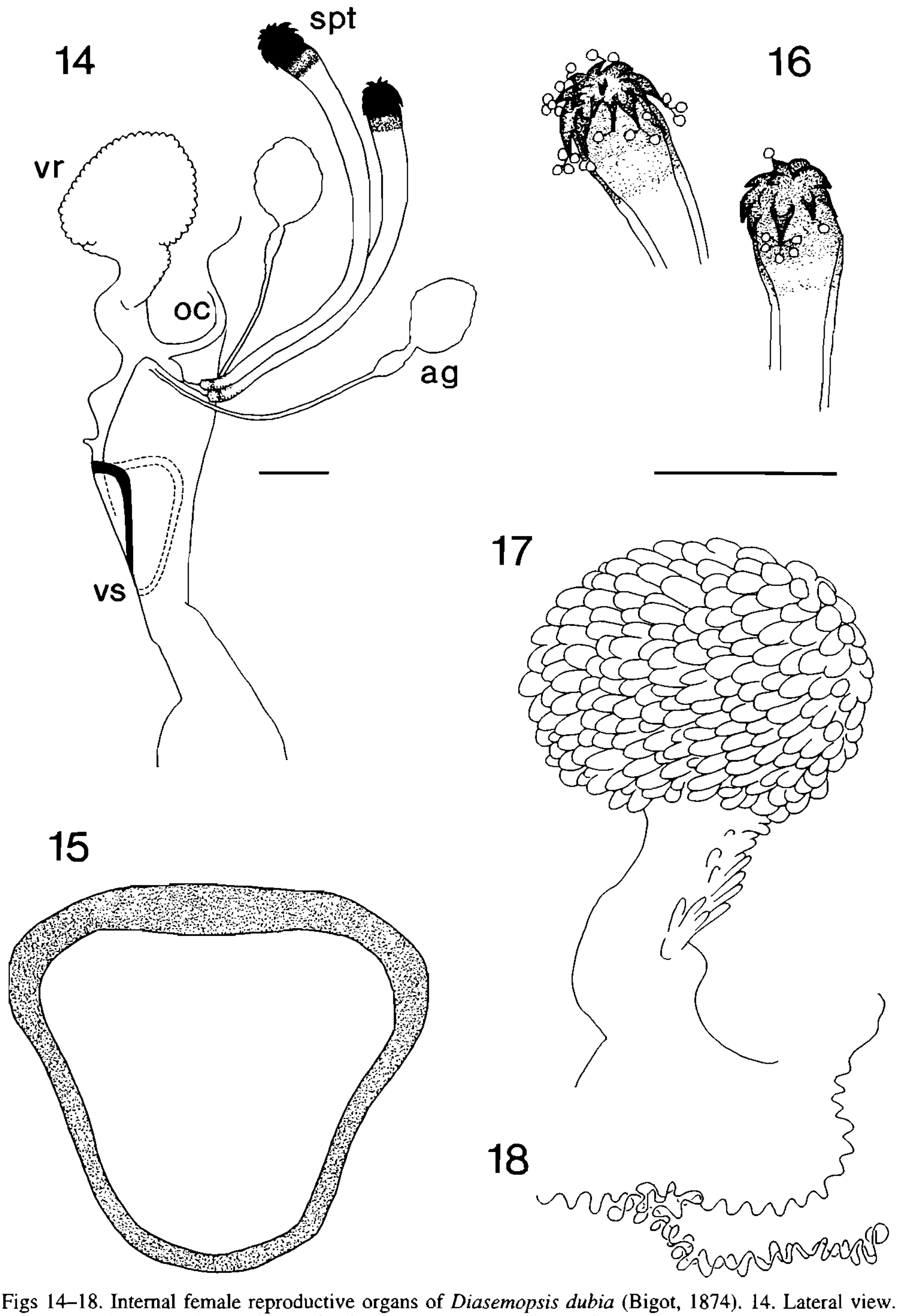
Chaetodiopsis is united with *Diasemopsis* by the enlargement of the ventral receptacle (6-1) and the reduced number of spermathecae (7-1). It is placed basal to *Diasemopsis* by plesiomorphic character states of spermathecae and spermathecal ducts (1-0, 2-1, 8-1). *Chaetodiopsis* is further characterised by very large spermathecae, that are shared with none of the other hitherto studied diopsids (Tan 1965, Tenorio 1969, Feijen 1981, 1984, 1986, Kotrba 1993).

Many features of the female reproductive tract of *Chaetodiopsis* and *Diasemopsis* are shared with other diopsid genera and are therefore plesiomorphies of the *Diasemopsis* genus group. The ornamentation of the spermathecae with pointed, hollow processes (9-1) is shared with various members of *Cyrtodiopsis* and *Teleopsis* (Tan 1965, Tenorio 1969, Feijen 1981 1989, Kotrba 1993). Yet the ornamentation is derived within the Diopsidae, as other genera such as *Diopsis* (see Feijen 1986, Tan 1965), *Diopsina* (see Feijen 1981) and the supposedly basal *Sphyracephala* (see Kumar 1978, Peterson 1987), have smooth spermathecae. Other plesiomorphic features of the *Diasemopsis* genus group are the multi-chambered organization of the ventral receptacle (10-1) and the occurrence of a ring-shaped sclerite in the ventral wall of the vagina (11-1), present in *Cyrtodiopsis whitei*, *Teleopsis quadriguttata* and many other Diopsidae as well (Tan 1965, Kotrba 1993 and unpublished data). The distribution of these characters in other Diopsidae will be discussed in a future publication.

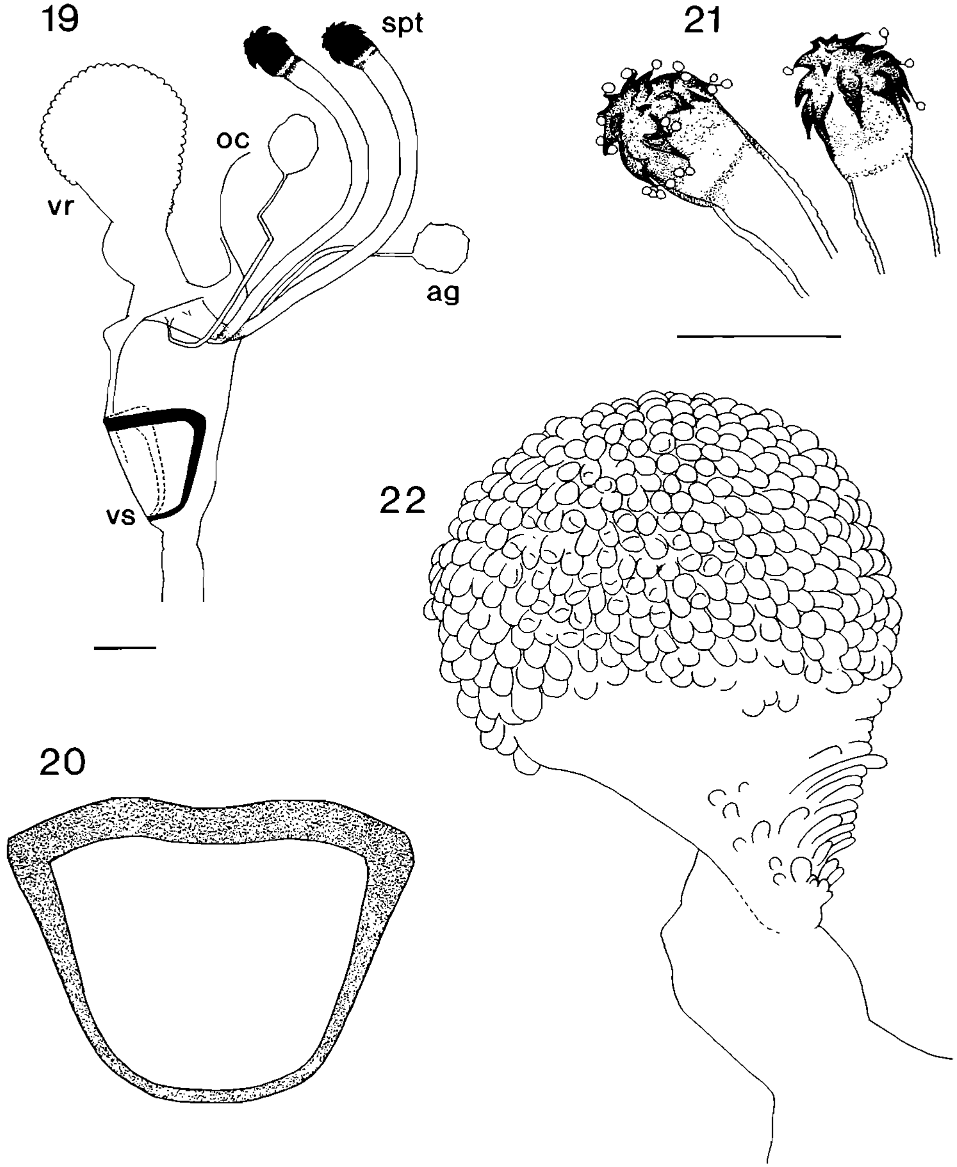
Aspects of functional morphology

The most remarkable innovation in the female reproductive organs of *Chaetodiopsis* and *Diasemopsis* is the enlargement of the multi-chambered ventral receptacle through elongation and multiplication of its chambers.

The possible adaptive values of a multi-chambered ventral receptacle *per se* have been discussed by Kotrba (1993). The numerous roundish chambers seem perfectly adapted to house individual coiled spermatozoa, as can be observed in fresh material. Furthermore, the parallel arrangement of the chambers can provide an arena for spermatozoon selection when spermatozoa compete for reaching the egg micropyle, which is positioned at the entrance of the organ for fertilization. The elongation of the chambers has apparently coevolved with an elongation of the spermatozoa as well. In *Diasemopsis dubia* the chambers of the ventral receptacle are more than tenfold longer (300-400 μm) than in *Cyrtodiopsis whitei* (17 μm) and other diopsid



Figs 14–18. Internal female reproductive organs of *Diasemopsis dubia* (Bigot, 1874). 14. Lateral view. 15. Ventral sclerite. 16. Spermathecae. 17. Ventral receptacle. 18. Spermatozoon. [Abbrevations: ag = accessory glands; oc = oviductus communis; spt = spermathecae; vr = ventral receptacle; vs = ventral sclerite. Scale bar = 100 μm, Figs 15–18 at same scale.]



Figs 19–22. Internal female reproductive organs of *Diasemopsis silvatica* Eggers, 1916. 19. Lateral view. 20. Ventral sclerite. 21. Spermathecae. 22. Ventral receptacle. [Abbrevations: ag = accessory glands; oc = oviductus communis; spt = spermathecae; vr = ventral receptacle; vs = ventral sclerite. Scale bar = 100 μm, Figs 20–22 at same scale.]

genera (Kotrba unpublished data), and the spermatozoa of *D. dubia* (> 1150 μm) are likewise much longer than those of *C. whitei* (178 μm). Coevolution of the length of spermatozoa and the female's sperm receptacle has been demonstrated also in the Drosophilidae (Hihara & Kurokawa 1987) and Ptiliidae (Coleoptera, Dybas & Dybas 1981).

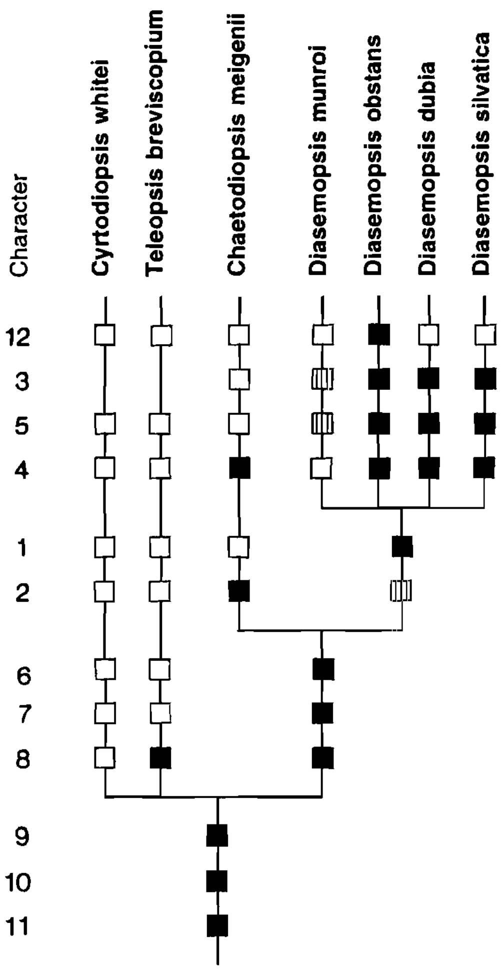


Fig 23. Strict consensus tree (length 13, ci 92, ri 90) calculated by Hennig 86 (Farris 1988) from characters coded in Table 1. Characters 3 and 8 were treated as unordered. [Empty squares: plesiomorphic condition (0), black and shaded squares: apomorphic conditions (1 and 2).]

The chambers of the ventral receptacle have not only been elongated, but their number has also been multiplied from about 60 in *Cyrtodiopsis whitei* and *Teleopsis quadriguttata* to several hundred in *Chaetodiopsis* and *Diasemopsis*. The ventral receptacle is thus capable of accommodating many more spermatozoa in the latter genera. At the same time the number of the original sperm storage organs, the spermathecae, has been reduced from three to two. Seemingly then, the ventral receptacle secondarily assumes the function of sperm storage. In *D. munroi* the very small spermathecae have probably lost most or all of their sperm storage function, whereas the glandular function is retained.

ACKNOWLEDGEMENTS

I thank Dr Brian Stuckenberg, Director *emeritus* of the Natal Museum, for hosting my stay at the museum in 1992. Dr David Barraclough, Mr Andrew Whittington and Mrs Shirley Robertson took me on several collecting trips and supported me in every possible way. Dr Gerald Wilkinson (University of Maryland) and Dr Wayne Mathis (United States National Museum of Natural History) hosted and supported me during the evaluation of the material and the writing of the manuscript. This part of the work was funded by a stipend of the German Scientific Foundation DFG. The excursion itself was financed by a generous donation from my father, Dr Walter Kotrba. Last but not least, I thank my colleagues at the United States National Museum of Natural History, especially Mr James Pakaluk, for their friendly support during the realisation of this paper.

REFERENCES

BURKHADT, D., DE LA MOTTE, I. & LUNAU, K. 1994. Signalling fitness: larger males sire more offspring. Studies of the stalk-eyed fly *Cyrtodiopsis whitei* (Diopsidae, Diptera). *Journal of Comparative Physiology*, Series A, **174**: 61—64.

BRUGGEN, A. C. VAN 1961. Diptera (Brachycera): Diopsidae. *In*: Hanstrom, B. *et al.* eds. *South African Animal Life, Results of the Lund University Expedition in 1950-1951*, Vol. 8: 415–439.

DYBAS, L. K. & DYBAS, H. S. 1981. Coadaption and taxonomic differentiation of sperm and spermathecae in featherwing beetles. *Evolution* **35**: 168–174.

EBERHARD, W. G. 1985. *Sexual selection and animal genitalia.* Cambridge: Harvard University Press.

FARRIS, J. S. 1988: Hennig 86, Version 1.5. New York: Port Jefferson Station.

FEIJEN, H. 1981. A review of *Diopsina* Curran, 1928 (Diptera: Diopsidae), with a note on *Cyrtodiopsis*. *Annals of the Natal Museum* **24**: 465–482.

——— 1984. *Diopsis nigrasplendens*, a new species of Diopsidae (Diptera). *Zoologische Mededelingen* **58**: 335–340.

——— 1986. A revision of the Diopsidae (Diptera) described by J. W. Dalman. *Entomologica Scandinavica* **17**: 409–422.

——— 1989. Diopsidae. *In*: Griffiths, G. C. D. ed. *Flies of the Nearctic Region*, Vol 9: 12. Stuttgart: Schweizerbart'scheVerlagsbuchhandlung.

GRIFFITHS, G. C. D. 1990. Review of *Manual of Nearctic Diptera*, Vol. 3. *Quaestiones Entomologicae* **26**: 117–130.

HENNIG, W. 1973. 31. Ordnung Diptera (Zweiflügler). *In*: Helmcke, J.-G. *et al.* eds. *Handbuch der Zoologie*, Vol. 4: 2, 2, 2. Berlin: De Gruyter.

HIHARA, F. & KUROKAWA, H. 1987. The sperm length and the internal reproductive organs of *Drosophila* with special references to phylogenetic relationships. *Zoological Science* **4**: 167–174.

KOTRBA, M. 1990. Sperm transfer by spermatophore in an acalyptrate fly (Diptera: Diopsidae). *Entomologia Generalis* **15**: 181–183.

——— 1993. Das Reproduktionssystem von *Cyrtodiopsis whitei* Curran 1936 (Diopsidae, Diptera) unter besonderer Berücksichtigung der inneren weiblichen Geschlechtsorgane. *Bonner Zoologische Monographien* **33**: 115 pp.

KUMAR, R. & NUTSUGAH, D. 1976. Alimentary and reproductive organs of *Diopsis thoracica*. *Annals of the Entomological Society of America* **69**: 190–194.

KUMAR, Y. 1978. Morphology of the external and internal genital organs of female *Sphyracephala hearseyana* Westw. (Diopsidae: Diptera). *Entomon* **3**: 201–205.

LA MUNYON, C. W. & EISNER, T. 1993. Postcopulatory sexual selection in an arctiid moth (*Utetheisa ornatrix*). *Proceedings of the National Academy of Sciences* **90**: 4689–4692.

MCALPINE, J. F. 1989. Phylogeny and classification of the Muscomorpha. *In*: McAlpine, J. F. & Wood, D. M. (eds). *Manual of Nearctic Diptera*, Vol. 3. Ottawa: Agriculture Canada, Research Branch. (Monograph; No. 32) pp. 1397–1518.

NOIROT, C. & QUENNEDY, A. 1974. Fine structure of insect epidermal glands. *Annual Review of Entomology* **19**: 61–80.

PETERSON, B. V. 1987. Diopsidae. *In*: McAlpine, J. F. *et al.* eds. *Manual of Nearctic Diptera*, Vol. 2. Ottawa: Agriculture Canada, Research Branch. (Monograph; No. 28) pp. 785–789.

SIMMONS, L. W. & PARKER, G. A. 1992. Individual variation in sperm competition success of yellow dung flies, *Scathophaga stercoraria*. *Evolution* **46**: 366–375.

SMITH, R. L., ed. 1984. *Sperm competition and the evolution of animal mating systems.* New York: Academic Press.

STEYSKAL, G. C. 1972. A catalogue of species and key to the genera of the family Diopsidae (Diptera: Acalyptratae). *Stuttgarter Beiträge zur Naturkunde* **234:** 1–20.

STURTEVANT, A. H. 1925. The seminal receptacles and accessory glands of the Diptera, with special reference to the Acalypterae. *Journal of the New York Entomological Society* **33**: 195–215.

——— 1926. The seminal receptacles and accessory glands of the Diptera, with special reference to the Acalypterae. *Journal of the New York Entomological Society* **34**: 1–21.

TAN, K. B. 1965. *Diopsidae*. BSc Honour's Thesis, University of Malaya, Kuala Lumpur.

TENORIO, J. A. 1969. A new species of *Teleopsis* Rondani from the Philippines (Diptera: Diopsidae). *Pacific Insects* **11**: 483–485.

WARD, P. I. 1993. Females influence sperm storage and use in the yellow dung fly *Scathophaga stercoraria* (L.). *Behavioral Ecology and Sociobiology* **32**: 313–319.

WILKINSON, G. S. & REILLO, P. R. 1994. Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. *Proceedings of the Royal Society of London*, Series B, **255**: 1–6.

Date received: 14 December 1994